Quinkana babarra, a New Species of Ziphodont Mekosuchine Crocodile from the Early Pliocene Bluff Downs Local Fauna, Northern Australia with a Revision of the Genus

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Willis, P.M.A. and Mackness, B.S. *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the Early Pliocene Bluff Downs Local Fauna, Northern Australia with a revision of the genus. Proc. Linn. Soc. N.S.W. 116, 143–151.

A new species of ziphodont mekosuchine crocodile, *Quinkana babarra* is described on the basis of a fragmentary right maxilla from the Early Pliocene Bluff Downs Local Fauna. This new crocodile differs from *Q. fortirostrum* and the recently described *Q. timara* in having: 1, a shorter snout; 2, palatal fenestrae only reaching to the level of the fifth and sixth maxillary alveoli and not the seventh as in *Q. fortirostrum*; 3, mild festooning and 4, teeth variously with or without serrations. Recognition of this new species necessitates the revision of the genus. Ingroup relationships of mekosuchines are obscure and the position of *Quinkana* within this subfamily cannot currently be determined.

Manuscript received 1 Mar 1994, accepted for publication 20 Jul 1995

KEYWORDS: Bluff Downs, crocodile, mekosuchine, *Quinkana*.

INTRODUCTION

Recent investigations of fossil crocodiles from Australia have revealed many more taxa than previously recognised (e.g. Willis and Archer 1990; Willis et al. 1990; Willis and Molnar 1991a, 1991b; Megirian et al. 1991; Willis 1992, 1993; Megirian 1994). These appear to represent a monophyletic Australian clade (Willis et al. 1990, Willis and Molnar 1991a) now recognised as the Mekosuchinae (Willis et al. 1993). There are a variety of ecomorphs among the mekosuchines including generalised, broad-snouted crocodilians (*Pallimnarchus* and *Australosuchus*), semi-ziphodont forms (*Baru*), fully ziphodont forms (*Quinkana*) and small terrestrial crocodilians (*Trilophosuchus* and *Mekosuchus*). Two longirostrine taxa may also be mekosuchines (Willis and Molnar 1991b; Megirian et al. 1991).

Australasian ziphodont crocodilians were initially reported by Plane (1967) and Hecht and Archer (1977). These were assigned to either sebecosuchian or pristicampsine crocodilians. Molnar (1977, 1978a, 1978b, 1981) described and named the almost complete snout of *Quinkana fortirostrum*. Molnar (1981) also described the fragmentary maxilla from Texas Caves that had been a focus of the study by Hecht and Archer (1977), two maxillary fragments and three teeth from Croydon, north Queensland and isolated teeth from a number of localities in Queensland. Megirian (1994) described a second species, *Q. timara* from the Miocene deposits of Bullock Creek, Northern Territory. This new species is distinctive in having an elongate snout.

A new species of a *Quinkana*, is described here from northeastern Queensland. This necessitates revision of the generic diagnosis of *Quinkana* Molnar 1981. The new species of *Quinkana* is the third crocodilian reported from the Early Pliocene Allingham

Formation, northwest of Charters Towers, northeastern Queensland. Archer (1976) reported the presence of teeth of *Pallimnarchus* sp. (QM F7763, QM F7764). Molnar (1979) described an incomplete snout of *Crocodylus porosus* (QM F9229). A large quantity of additional crocodile material since recovered will be described (B.M) as part of a comprehensive study of the Bluff Downs Local Fauna in progress. The Allingham Formation appears to represent freshwater fluviatile and lacustrine deposits. A number of Early Pliocene taxa have been previously reported from the deposit including mammals, birds, reptiles and fish (Archer 1976, Bartholomai 1978, Archer and Dawson 1982, Archer 1982, Rich and Van Tets 1982, Vickers-Rich 1991, Mackness et al. 1993, Boles and Mackness 1994, Mackness 1995(a), Mackness 1995(b)). Collectively the Early Pliocene Allingham assemblage has been called the Bluff Downs Local Fauna (Archer 1976).

Osteological terminology follows Romer (1956) and Steel (1973). Abbreviations for specimen numbers: AM F, Australian Museum fossil collection; QM F, Queensland Museum fossil collection.

SYSTEMATICS

Order Crocodylia Gmelin, 1788
Suborder Eusuchia Huxley, 1875
Family Crocodylidae Cuvier, 1807
Subfamily Mekosuchinae Balouet and Buffetaut, 1987
Genus *Quinkana* Molnar, 1981

Molnar's (1981) original definition of *Quinkana* was based on the single species *Q. fortirostrum*. Molnar (1981) reported that no portion of the jugal extended anterior to the orbit and included this feature in the diagnosis of *Quinkana*. Re-examination of the type specimen of *Q. fortirostrum* (AM F57844) however, reveals that the jugal does extend anterior to the orbit. The anterior portion of the jugal can only be seen on the interior surfaces of the snout; the external surfaces are heavily sculptured, obscuring this and some other sutural contacts. Megirian (1994) claims that the external sutural contacts in this region can be traced but we have difficulty in recognising them. The jugal-maxillary contact in crocodiles, however, is diagonal in cross section such that the exterior expression of the jugal-maxillary contact is always anterior to the interior expression of the suture. Because the interior expression of the jugal-maxillary suture is anterior to the orbit, the exterior expression of this contact must be located even further towards the anterior.

Megirian (1994) revised the generic definition of *Quinkana* as part of his description of *Q. timara*. The following revision does not violate any of his generic determinations and extends the concept of *Quinkana* to accommodate the new species described here.

Revision of the genus *Quinkana*:

The following features were given by Molnar in his diagnosis of *Q. fortirostrum*: three knobs present on lacrimal and prefrontal dorsal to the anterior to the margin of the orbit; orbit rim superiorly adjacent or anterior to the margin of the palatal fenestrae.

The following revised generic features define *Quinkana*, apomorphies identified by (a): mekosuchine crocodilians with moderately deep snout; (a) alveoli elongate and arranged with the cross-sectional long axis aligned to the tooth row; palatal portion of the maxillary-premaxillary suture U-shaped with convexity directed posteriorly; maxillary alveoli subequal in size; (a) distinct alveolar process with a series of dentary tooth reception pits along the medial side; festooning suppressed; (a) snout trapezoid in cross section immediately anterior to the orbits; anterior process of palatine very short or absent.

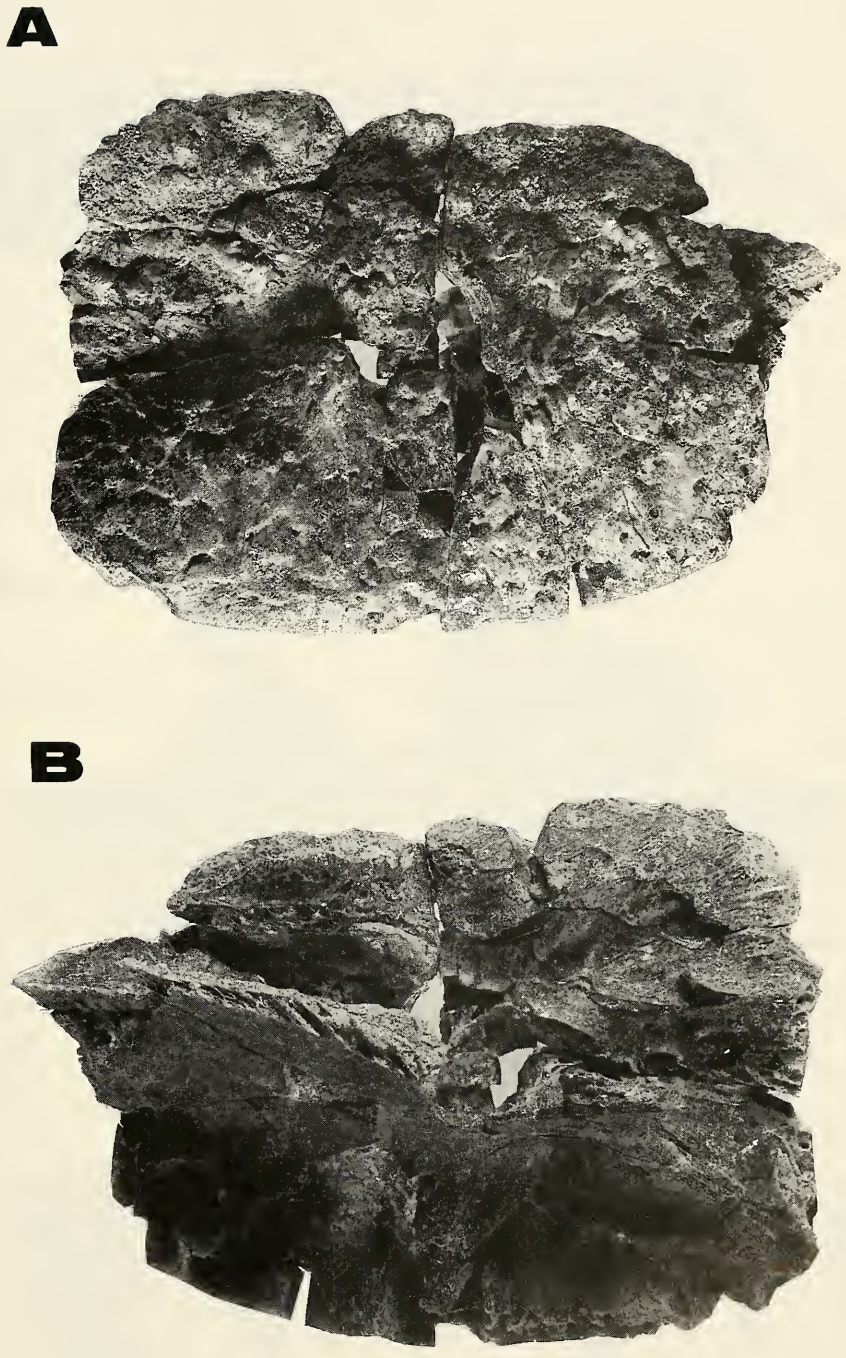

Fig. 1. Quinkana barbarra sp. nov. holotype QM F23220. Right maxilla. Actual size. A, buccal; B, lingual.

Crocodilans are remarkably conservative in form and regularly display convergence and parallel evolution. We have used a suite of characters including autapomorphies, generic synapomorphies and allometric characters to more clearly delineate a specific and generic diagnoses. Autapomorphies have been clearly marked in the diagnosis and the inclusion of the additional characters in the diagnosis is justified on the basis of clarification of our revised generic concept of *Quinkana*.

Knobs on the lacrimals and prefrontals, anterior shelves, suborbital jugal sulci and palatal buldges, as noted for *Q. fortirostrum* and *Q. timara*, are not known for *Q. babarra* and have been removed from the generic diagnosis.

Quinkana babarra n. sp. (Figs. 1–2)

Holotype

QM F23220, a partial right maxilla and associated fragments collected by Brian Mackness and colleagues in 1991.

Referred specimens

QM F23221–F23223, isolated ziphodont teeth. (Fig. 2).

Type locality

Dick's Mother Lode Quarry, Allingham Formation (Lat. 19°42′67″S, Long. 145°36′06″E), Bluff Downs Station, northeastern Queensland.

Age

Early Pliocene based on the interpreted age of the overlying Allensleigh basalt (Archer and Wade 1976).

Entmology

The specific name is from a Gugu-Yalanji dialect word *babarr*, meaning 'older sister' (Oates et al. 1964) and is used to denote the relationship of this crocodile to *Q. fortirostrum*.

Diagnosis

Quinkana babarra has a shorter, broader snout with mild festooning compared to *Q. fortirostrum* and *Q. timara* which have no festooning. *Quinkana babarra* is slightly smaller than the holotype (AM F57844) of *Q. fortirostrum* and NTM P895–19, the holotype maxilla of *Q. timara*. The palatal fenestrae in *Q. babarra* reach anteriorly to the level of the fifth and sixth maxillary alveoli but they only extend to the level of the seventh maxillary alveolus in *Q. fortirostrum* and the eighth maxillary alveolus in *Q. timara*. The lateral and upper surfaces of the maxilla are not as heavily sculptured as in *Q. fortirostrum* but are comparable to those of *Q. timara*. The sculpture on the lateral surface is less than on the dorsal surface where the bone rises into isolated small peaks. There is a larger peak in the antero-dorsal corner of the maxilla near the nasal-maxillary-premaxillary junction. In *Q. fortirostrum* this peak forms the postero-medial terminus of a low, rounded crest that extends obliquely across the maxilla onto the premaxilla above the fourth dentary tooth reception notch. This crest is poorly developed and only on the maxilla of *Q. timara*.

There is a pronounced trough on the posterior of the dorsal surface that extends anteriorly to the level of the fifth alveolus and posteriorly beyond the edge of the fragment as preserved. A similar but much less pronounced trough is present on *Q. fortirostrum*. *Quinkana babarra* is similar to *Q. fortirostrum* and *Q. timara* in having laterally compressed alveoli but these are arranged with the long axes in line with each other (in *Q. fortirostrum* and *Q. timara* each axis is slightly oblique). The alveoli are located on a narrow alveolar process with dentary tooth reception pits on the medial side. The alveoli indicate a degree of homodonty comparable to that of *Q. fortirostrum*. The total maxillary alveoli count is unknown in *Q. babarra* and *Q. timara* whereas in *Q. fortirostrum* it is twelve. The carinae of teeth in *Q. babarra* are variously with or without serrations in distinction from those of *Q. fortirostrum* and *Q. timara* which have serrate carinae.

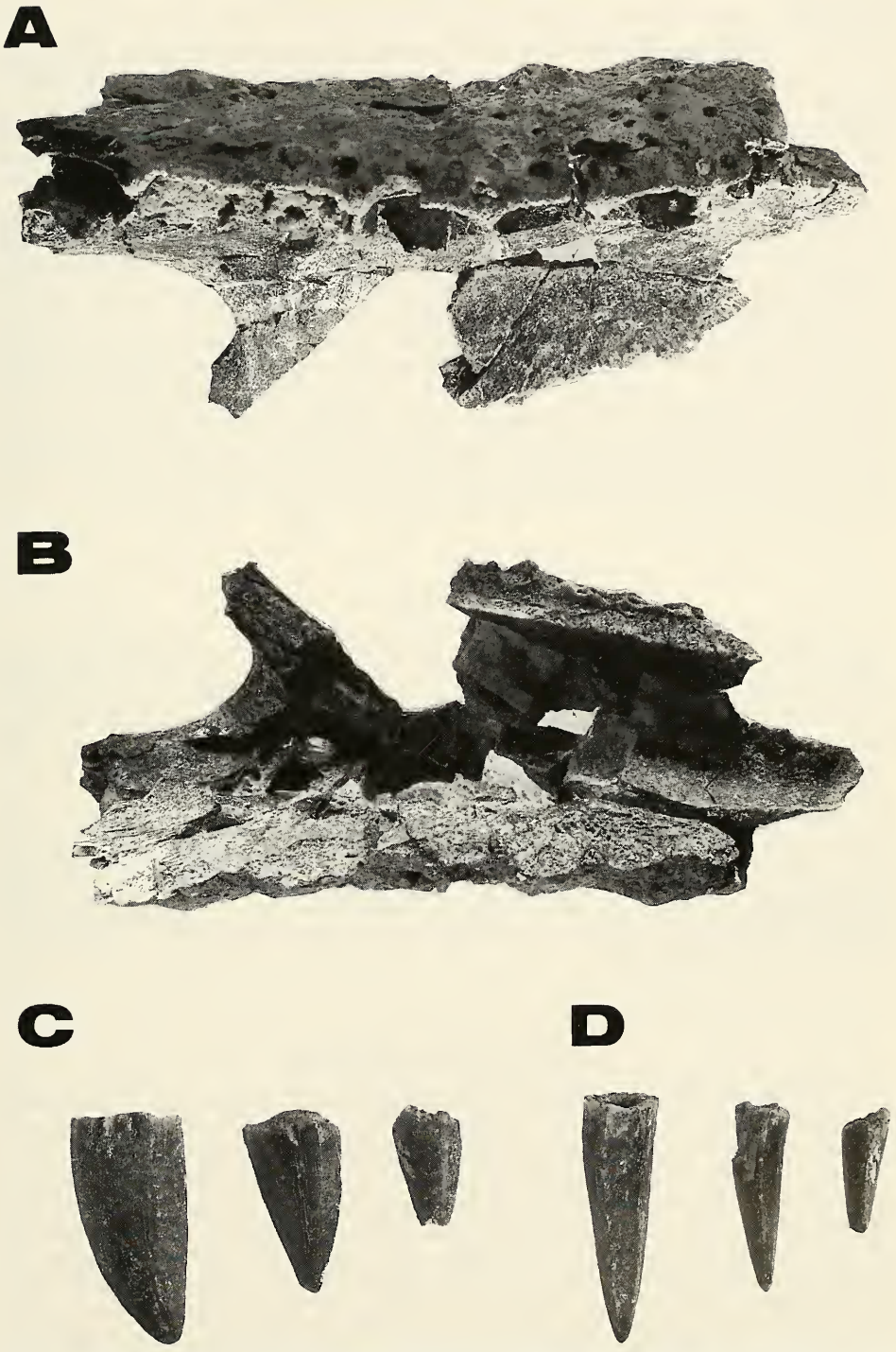

Fig. 2. Quinkana barbarra sp. nov. holotype QM F23220. Right maxilla. Actual size. A, ventral; B, dorsal. Isolated ziphodont crocodile teeth QM F23221–F23223 referred to *Q. babarra*. C, lateral; D, mesial.

Description

The holotype (Figs. 1, 2) is the only known specimen consisting of the anterior portion of the right maxilla and some associated fragments. The maxilla is reasonably complete, anterior to the fifth alveolus but the posterior extent is not preserved. There is almost a total suppression of festooning but the curvature of the tooth row in lateral view between the first and sixth alveoli is more pronounced than in *Q. fortirostrum* and *Q. timara*.

The palatal fenestra reaches anteriorly to a level between the fifth and sixth alveoli, almost to the level of the large nutrient foramina medial to the fifth alveolus. There is no indication of an anterior process of the palatine despite most of the palatal portion of the maxilla being preserved. The palatal junction with the premaxilla would have described a broad U-shaped suture similar to that of *Q. fortirostrum* and *Q. timara*.

Isolated ziphodont teeth from Bluff Downs (Fig. 2), are tentatively referred here to *Q. barbarra*. A single ziphodont tooth crown found as a fragment associated with the type specimen cannot be unambiguously shown to be part of that individual. As a consequence, it too is tentatively referred to *Q. babarra*. All ziphodont teeth from Bluff Downs exhibit lateral compression and anterior and posterior carinae. The carinae are serrate on some teeth but not on others. All teeth are mildly recurved such that the anterior carina is longer than the posterior carina. The posterior carina is mildly convex in profile.

COMPARISONS

Molnar (1981) referred a number of fragmentary maxillae and isolated teeth to *Quinkana* sp. because they were too incomplete to compare with the holotype of *Q. fortirostrum*. Similarly, an incomplete maxilla from Glen Garland Station, referred to in a note added in proof by Molnar (1981), could not be conclusively assigned by him to *Q. fortirostrum* but did show some differences in alveolar form and orientation. However, none of the fragmentary skull material referred to *Quinkana* sp. by Molnar (1981) exhibits the suite of diagnostic features that characterise *Q. babarra*.

The Glen Garland specimen does have an arrangement of alveoli similar to that seen in *Q. babarra*, a feature in which they both differ from *Q. fortirostrum* and *Q. timara*. This feature could represent intraspecific variation. Other characters, such as the anterior extent of palatal fenestrae cannot be determined on the Glen Garland specimen. For these reasons, we conclude that this specimen should be regarded as *Quinkana* sp. until better material is known.

PHYLOGENETIC AFFINITIES

Detailed phylogenetic analysis of the Mekosuchinae conducted by Willis (1995) and Salisbury and Willis (in press) confirm the mekosuchine affinites of *Quinkana* contrary to the possible pristichampsine affinites considered by Mergirian (1994). The phylogenetic affinities of the genus *Quinkana* are considered here with respect to other mekosuchines. Willis et al. (1990) recognised, but did not name, the clade of Australian Tertiary crocodiles that included *Baru*, *Pallimnarchus* and *Quinkana*. Willis and Molnar (1991a) expanded this concept to include the new genus *Australosuchus* and recognised additional synapomorphies for the clade. An unnamed Eocene crocodilian from south-eastern Queensland described by Willis and Molnar (1991b) appears to belong to the same clade but is represented by fragmentary material. Similarly, *Harpocochampsa*, a longirostrine crocodilian from Miocene sediments in the Northern Territory (Megirian et al. 1991) exhibits insufficient features to support or refute its assignment to the

Mekosuchinae. *Trilophosuchus*, from Miocene deposits at Riversleigh, northwestern Queensland (Willis 1993) is a small, terrestrial carnivore that also clearly belongs within the Australian clade.

It was not until the description of *Kambara*, a crocodilian from the early Eocene Murgon sediments of southeastern Queensland (Willis et al. 1993), that the Australian Tertiary crocodilian clade was formally named the Mekosuchinae. The small terrestrial Holocene crocodilian *Mekosuchus inexpectatus* from New Caledonia has also been included in the Mekosuchinae (Willis et al. 1993). There are now six genera within the Mekosuchinae. Unfortunately some genera are represented by fragmentary material and only two species are represented by almost complete skulls. This paucity of complete material has hampered efforts to identify characters that could resolve intergeneric relationships within the Mekosuchinae. Further, the species of *Quinkana* are the only truly ziphodont mekosuchines and their derived condition obscures the interpretation of character states that would otherwise be useful in determining their relationship to other members of the Australian clade.

Three mekosuchine genera (*Quinkana*, *Trilophosuchus* and *Mekosuchus*) are demonstrably terrestrial (Molnar 1981, Balouet and Buffetaut 1987, Willis 1993, Willis 1995, Salisbury and Willis in press), and these taxa appear to form a monophyletic clade. Both species of *Trilophosuchus* and *Mekosuchus* have short deep snouts reminiscent of atoposaurids, species of *Quinkana* have a longer snout that is more reminiscent of species of *Baru* than of the smaller mekosuchines. Species of *Baru* and *Quinkana* share a snout form that is trapezoid in cross section anterior to the orbits, a feature not characteristic of species of *Trilophosuchus* or *Mekosuchus*.

A fourth species of *Quinkana* from Miocene deposits at Riversleigh, along with other mekosuchines, is currently being described (P.W). Isolated teeth have been referred to *Quinkana* have been recorded from the mid Miocene Ongeva Local Fauna (Megirian et al. 1993, Murray et al. 1993) and the Pleistocene Wyandotte Local Fauna (McNamara 1990).

PALAEOECOLOGY

Ziphodont crocodiles have been found in South America, North America, Europe, Asia and Africa as well as in New Guinea and Australia (Langston 1956, Langston 1975, Plane 1967, Molnar 1981). Nearly complete skeletons of ziphodont crocodilians have been described from Europe (Kuhn 1938, Berg 1966). The hoof-like terminal phalanges and extensive development of armour in these species have been interpreted as a possible indication of terrestrial specialisation (see Kuhn 1938, Zappler 1960, Steel 1973). Molnar (1981) summarised the conditions of deposition of ziphodont fossils and all, except for a few cave fills, are near water environments. Molnar raised the problem of the association of ziphodont crocodiles with lacustrine or fluvial deposition and the notion of terrestriality but concluded that *Q. fortirostrum* was probably terrestrial. The palaeoecology of the Bluff Downs site has been interpreted as being a freshwater fluviatile and lacustrine deposit (Archer and Wade 1976).

Busbey (1986), while noting the depositional association problems raised by Molnar (1981), supported the notion of terrestriality using ziphodont cranial morphology which he interpreted to be convergent on terrestrial reptilian carnivores such as *Varanus komodoensis*. Several authors (Archer and Bartholomai 1978, Molnar 1981) have suggested an absence of very large terrestrial mammalian predators in Australian Tertiary and Pleistocene deposits as a possible reason for this niche being occupied by large reptiles such as species of *Quinkana* and *Megalania*. Remains of a large varanid have been recovered from the Bluff Downs site (Archer 1976) as well as several mammalian predators including *Thylacoleo crassidentatus* (Archer and Dawson 1982). *Quinkana babarra* is shown to be a large, terrestrial, reptilian, carnivore in the Bluff

Downs Fauna. Its presence, along with that of other large reptilian carnivores and the apparent absence of large mammalian carnivores, represents a fundamentally different structure to the large carnivore niches typical of modern faunas. The Bluff Downs Local Fauna is complete enough and demonstrates suitable diversity to allow a more thorough investigation of the structure and function of large terrestrial reptilian predators within a faunal context. The palaeoecology of the Bluff Downs Local fauna is the subject of ongoing study (B.M.).

ACKNOWLEDGEMENTS

The authors wish to thank Ralph E. Molnar, Michael Archer, Suzanne Hand, John Scanlon and Jeanette Muirhead for their helpful comments on the manuscript. Jeffrey Wright kindly provided the photographs. Joanne Wilkinson provided technical back-up. Jack, Rhonda, Bram, Troy and Selesti Smith of Bluff Downs Station provided vital support for the ongoing research into the Bluff Downs Local Fauna. The collection of the Bluff Downs material was supported in part by: an ARC Program Grant to M. Archer; a grant from the Department of Arts, Sport, the Environment, Tourism and Territories to M. Archer, S. Hand and H. Godthelp; a grant from the National Estate Program Grants Scheme, Queensland to M. Archer and A. Bartholomai; and grants in aid to the Riversleigh Research Project from Wang Australia, ICI Australia and the Australian Geographic Society.

REFERENCES

Archer, M. (1976). Bluff Downs local fauna. *Memoirs of the Queensland Museum* **17**, 383–396.

Archer, M. (1982). Review of the dasyurid (Marsupialia) fossil record, integration of data on phylogenetic interpretation, and suprageneric classification. In 'Carnivorous marsupials' (Ed. M. Archer) pp. 397–443. (Royal Zoological Society of New South Wales, Sydney).

Archer, M. and Bartholomai, A. (1978). Tertiary mammals of Australia: a synoptic view. *Alcheringa* **2**, 1–19.

Archer, M. and Dawson, L. (1982). Revision of marsupial lions of the genus *Thylacoleo* Gervais (Thylacoleonidae, Marsupialia) and Thylacoleonid evolution in the late Cainozoic. In 'Carnivorous marsupials' (Ed. M. Archer) pp. 477–494. (Royal Zoological Society of New South Wales, Sydney).

Archer, M. and Wade, M. (1976). Results of the Ray E. Lemley Expeditions, Part I. The Allingham Formation and a new Pliocene vertebrate fauna from northern Australia. *Memoirs of the Queensland Museum* **17**, 379–397.

Bartholomai, A. (1978). The Macropodidae (Marsupialia) from the Allingham Formation, Northern Queensland. Results of the Ray E. Lemley Expeditions, Part 2. *Memoirs of the Queensland Museum* **18**, 127–143.

Balouet, J.C. and Buffetaut, E. (1987). *Mekosuchus inexpactatus* n.g. n. sp. Crocodilien nouveau de l'Holocene de Nouvelle Caledonie. *Comptes Rendus des séances de l'Académie des Science, Paris* **304**, 853–857.

Berg, D.E. (1966). Die Krokodile, insbesondere *Asiatosuchus* ubd aff. *Sebecus*? aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **52**, 1–105.

Boles, W.E. and Mackness, B.S. (1994). Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland. *Records of the South Australian Museum* **27**, 139–149.

Busbey, A.B. (1986). New material of *Sebecus* cf *huilensis* (Crocodilia: Sebecosuchidae) from the Miocene La Vanta Formation of Columbia. *Journal of Vertebrate Paleontology* **6**, 20–7.

Hecht, M.K. and Archer, M. (1977). Presence of xiphodont (sic) crocodiles in the Tertiary and Pleistocene of Australia. *Alcheringa* **1**, 383–85.

Kuhn, O. (1938). Die Crocodilier aus dem mittleren Eozän des Geiseltales bei Halle. *Nova Acta Leopoldina (N.F.)* **6**, 313–29.

Langston, W. (1956). The Sebecosuchia: cosmopolitan crocodiles? *American Journal of Science* **254**, 605–14.

Langston, W. (1975). Ziphodont crocodiles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. *Fieldiana: Geology*. **33**, 291–314.

Mackness, B.S. (1995)a. *Anhinga malagurala*, a new pygmy darter from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. *Emu*. **95**, 265–71.

Mackness, B.S. (1995)b. *Palorchestes selestiae*, a new species of palorchestid marsupial from the early Pliocene Bluff Downs Local Fauna, northeastern Queensland. *Memoirs of the Queensland Museum*. **38**, 603–609.

Mackness, B.S., Archer, M., and Muirhead, J. (1993). An enigmatic family of marsupials from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland. CAVEPS '93; Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics. Adelaide, 19–21 April 1993. Programme and Abstracts.

McNamara, G. (1990). The Wyandotte Local Fauna: a new, dated, Pleistocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum* **28**, 285–297.

Megirian, D. (1994). A new species of *Quinkana* Molnar (Eusuchia: Crocodylidae) from the Miocene Camfield Beds of Northern Australia. *The Beeagle, Records of the Norther Territory Museum of Arts and Science* **11**, 145–166.

Megirian, D., Murray, P.F. and Wells, R.T. (1993). The late Miocene Ongeva Local Fauna from the Waite Formation of Central Australia. CAVEPS '93; Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics. Adelaide, 19–21 April 1993. Programme and Abstracts.

Megirian, D., Murray, P.F. and Willis, P.M.A. (1991). A new crocodile of the gavial ecomorph morphology from the Miocene of northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **8**, 135–158.

Molnar, R.E. (1977). Crocodile with laterally compressed snout; first find in Australia. *Science* **197**, 62–4.

Molnar, R.E. (1978)a. The crocodile from Tea Tree Caves and ziphodont crocodiles in Australia. *Journal of the Sydney Speological Society* **22**, 3–10.

Molnar, R.E. (1978)b. Age of the Chillagoe crocodile. *Search* **9**, 156–8.

Molnar, R.E. (1979.) *Crocodylus porosus* from the Pliocene Allingham Formation of North Queensland. Results of the Ray E. Lemley Expeditions, Part 5. *Memoirs of the Queensland Museum* **19**, 357–65.

Molnar, R.E. (1981). Pleistocene ziphodont crocodilians of Queensland. *Records of the Australian Museum* **33**, 803–34.

Murray, P. and Megirian, D. (1992). Continuity and contrast in Middle and Late Miocene vertebrate communities from the Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **9**, 195–218.

Murray, P., Megirian, D. and Wells, R. (1993). *Kolopsis yperus* sp.nov. (Zygomaturinae, Marsupialia) from the Ongeva Local Fauna: New evidence for the age of the Alcoota fossil beds of Central Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **10**, 155–172.

Oates, W., Oates, L., Hershberger, H., Hershberger, R., Sayers, B. and Godfrey, M. (1964.) *Gugu-Yalangi and Wik-Munkan language studies*. Occasional Papers in Aboriginal Studies. Number Two. Australian Institute of Aboriginal Studies.

Plane, M.D. (1967). Stratigraphy and vertebrate fauna of the Otibanda Formation, New Guinea. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* **86**, 1–64.

Rich, P.V. and van Tets, G.F. (1982). Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. In 'The Fossil Vertebrate Record of Australasia' (Eds. P.V. Rich and E.M. Thompson, E.M.). pp. 235–384. (Monash University Offset Printing Unit: Clayton).

Romer, A.S. (1956). 'Osteology of the Reptiles'. (University of Chicago Press: Chicago).

Salisbury, S. and Willis, P.M.A. (in press). A new crocodylian from the early Eocene of southeastern Queensland and a primary investigation into the phylogenetic relationships of crocodyloids. *Alcheringa*.

Steel, R. (1973). Crocodylia. In 'Encyclopedia of Paleoherpetology' (Ed. O. Kuhn) Part 16. (Gustav Fisher Verlag: Stuttgart).

Vickers-Rich, P. (1991). The Mesozoic and Tertiary History of Birds on the Australian Plate. In 'Vertebrate Palaeontology of Australasia' (eds. P. Vickers-Rich, J.M. Monaghan, R.F. Baird, R.F. and T.H. Rich) pp. 721–808. (Pioneer Design Studio: Lilydale).

Willis, P.M.A. (1992). Four new crocodilians from early Miocene sites at Riversleigh Station, northwestern Queensland. *The Beagle, Records of the Northern Territory Museum of Arts and Science* **9**, 269.

Willis, P.M.A. (1993). *Trilophosuchus rackhami gen. et sp. nov.*, a new crocodilian from the early Miocene limestones of Riversleigh, northwestern Queensland. *Journal of Vertebrate Paleontology* **13**, 90–8.

Willis, P.M.A. (1995). The phylogenetic systematics of Australian crocodilians. PhD thesis, University of New South Wales, Sydney.

Willis, P.M.A. and Archer, M. (1990). A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Krefft. *Memoirs of the Queensland Museum* **28**, 159–63.

Willis, P.M.A., Murray, P.F. and Megirian, D. (1990). *Baru darrowi gen. et sp. nov.*, a large, broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in northern Australia. *Memoirs of the Queensland Museum* **29**, 521–40.

Willis, P.M.A. and Molnar, R.E. (1991)a. A new middle Tertiary crocodile from Lake Palankarinna, South Australia. *Records of the South Australian Museum* **25**, 39–55.

Willis, P.M.A. and Molnar, R.E. (1991)b. A longirostrine crocodile from the early Tertiary of southeastern Queensland. *Alcheringa* **15**, 229–33.

Willis, P.M.A., Molnar, R.E. and Scanlon, J.D. (1993). An early Eocene crocodilian from Murgon, southeastern Queensland. *Kaupia: Darmstädter Beitrage zur Naturgeschichte* **3**, 25–32.

Zappler, G. 1960. Fossil bonanza. *Natural History* **69**, 18–31.